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Early Growth Characteristics of Planted Deerbrush and Greenleaf Manzanita Seedlings in California

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As forest management shifts toward the management, sustainability, and restoration of ecosystems,[1] the need for knowledge on many species is increasingly critical. The often uneconomic and sometimes inconspicuous shrubs, forbs, and grasses are being recognized for increased ecological, wildlife, scenic, and erosion-control values.

O'Hara and others[2] noted that future forestry must embrace "a mix of commercially valuable and nonvaluable species," and "respond to the requirements of constituent species." Aune and others[3] suggested that greater within-stand species variation will be desired in the future and "the growing and planting of high-quality seedlings of hardwood trees, shrubs, and other flowering plants is now expanding to meet multi-resource objectives." Hungerford[4] stated that, "additional research is needed on seed dissemination and establishment requirements for many species," and Rietveld[5] noted an increased demand for diverse tree and shrub nursery stock, especially for species that provide food and shelter for wildlife.

Deerbrush (*Ceanothus integerrimus* H. & A.) and greenleaf manzanita (*Arctostaphylos patula* Greene) are two shrub species that are widespread and overlap in most of their natural ranges in California. Deciduous deerbrush is found throughout the Cascade Range of Oregon, all major mountain ranges of California, two mountainous areas in Arizona, and one locale in western New Mexico.[6] Deerbrush is an early successional species that becomes prevalent on sites that have been disturbed by logging or burning. Here the species grows well until eventually shaded out by trees. Deerbrush maintains its presence on the site, however, by a "bank" of viable, but dormant, seed in the soil.

Deerbrush often dominates in young conifer plantations,[7] probably because it can maintain high stomatal conductances and high photosynthesis rates at substantially lower plant and soil water potentials than associated conifers. Indeed, photosynthetic rates approached their seasonal maxima at plant water potentials as low as -25 to -30 bars in the central Sierra Nevada.[8] Deerbrush can withstand both cold and hot temperature extremes and poor site conditions.[6] On poor sites, it often fixes nitrogen, and on good sites it occasionally does. Deerbrush is classified as "preferred" browse for wildlife,[9] and as "the most important forage plant in part of the ponderosa pine belt in California."[10]

Evergreen greenleaf manzanita ranges throughout the Cascade Mountain Range from Washington southward through California. It also is found in all other California mountain ranges and extends southward into Baja California.[11] The species is more intolerant of shade and more upright in form than deerbrush. It also is well adapted to a hot, dry, climate; poor soils; and temperature extremes.[12,13] Like deerbrush, it is an early successional species that sprouts from the root crown and originates from dormant seed in the soil. Thousands of seedlings per hectare are common after a disturbance. Greenleaf manzanita produces large seed crops every other year, and its berries are prime food for a host of animals. The foliage is "reasonably good" for browse.[14]

On the basis of their widespread distribution, inclusion in many plant communities, rapid covering of the ground, and wildlife value, it is likely that deerbrush and greenleaf manzanita will be considered for planting in certain forested areas. Although some information is available on seed production, storage, and germination

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On a productive site in northern California, deerbrush (*Ceanothus integerrimus*) and greenleaf manzanita (*Arctostaphylos patula*) were grown in a nursery and outplanted in a clearing on the Shasta-Trinity National Forest. Survival, phenology, and growth characteristics were quantified from 1992 to 1995. In 1995, survival of deerbrush was 83 percent, and that of manzanita, 89 percent—values that did not change after the first growing season. Deerbrush plants developed multiple stems from the root crown during the first growing season; manzanita did so during the second. After two growing seasons, deerbrush plants had significantly more stems, were taller plants, and had wider crowns than plants of greenleaf manzanita. Deerbrush began flowering during the third growing season when 42 percent of plants produced flowers and seed. This proportion increased to 77 percent the fourth season. Greenleaf manzanita did not flower during the study.

Retrieval Terms: artificial regeneration, deerbrush, development, flowering, greenleaf manzanita, survival, northern California,

requirements of *Ceanothus* and *Arctostaphylos* species,[15] little is known about the magnitude and timing of seedling development, especially of planted seedlings. For deerbrush, "no published data are available on the age when seed production begins," and "few data are available on the growth rates of sprouting shrubs."[6] Similar data are lacking for greenleaf manzanita.

This note presents information on survival, number of stems per plant, stem height, crown width, and phenology for artificially regenerated deerbrush and greenleaf manzanita in California, and statistically examines these data for differences between the two species.

Methods

The study area is located in a portion of the Redhill progeny site on the Mount Shasta Ranger District of the Shasta-Trinity National Forests, and about 8 km southwest of Mount Shasta, California. As such, the ground was free of trees and shrubs, but covered with forbs and grasses when the study began. The area also was surrounded by a 2.4-m tall wire-mesh fence to eliminate damage from deer and rabbits.

Before the area became a progeny site, it supported a mixed conifer-hardwood forest composed of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws. var. *ponderosa*), California white fir (*Abies concolor* var. *lowiana* [Gord.] Lemm.), coast Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *menziesii*), sugar pine (*Pinus lambertiana* Dougl.), incense-cedar (*Libocedrus decurrens* Torr.), and California black oak (*Quercus kelloggii* Newb.). Mature plants of greenleaf manzanita and deerbrush were present between trees and in small openings.

After the study area was designated, it was manually cleared (hand tools) of all vegetation, and a drip irrigation system was installed. All competing woody and herbaceous vegetation was grubbed twice each year during the 1992-1995 study period.

Site quality of the study area is high, with height of dominant mixed conifers averaging 20 m in 50 years.[16] The soil, which is closely related to the Asta series, is formed in volcanic ash deposited over glacial outwash from pyroclastic materials. It has a sandy loam texture grading to loam with depth, and is at least 2 m deep. The elevation is 1100 m, the slope is 3 percent, and the aspect is northeast. Precipitation averages about 1016 mm per year, with about 70 percent falling as snow. Temperatures range from -7 °C, to 35 °C with the average annual temperature being about 10 °C. The growing season is 120 days.

Because this study was part of a larger study on interspecific root competition,[17] ponderosa pine and Douglas-fir seedlings were planted in the study area in spring 1990 at a spacing of 2 by 2 m. Deerbrush and greenleaf manzanita seedlings were planted 30 to 46 cm from each conifer seedling in spring 1992, and although competition occurred, it is best described as light.

Deerbrush and greenleaf manzanita seedlings in small peatpots were purchased from a commercial nursery. The peatpots were 8 cm square and 10 cm deep. The seed source for both species was near the study area and within the correct elevational zone. Seedlings were 5 to 10 cm tall and of healthy appearance at time of planting. In May 1992, each shrub seedling was outplanted as a plug (bottom of container removed) in a drilled hole, 46 cm deep, which was backfilled with soil and peatmoss. The seedlings were irrigated every 10 days for 6 weeks. Fertilizer (15-30-15) was included in the irrigation water. Seedlings were neither irrigated nor fertilized after 6 weeks so that they could become acclimatized to the natural environment.

Because of minor differences in slope and aspect, the experimental design was randomized block with three blocks. The area occupied by each shrub species in each block was called a plot. A plot consisted of about 0.05 ha on which 35 to 40 shrub seedlings were surrounded by at least one row of buffer (seedlings of similar species). In each plot, 25 seedlings were randomly selected for study and permanently tagged. On each of the sample seedlings, number of sprout stems per plant, crown diameter (measured in two directions and averaged), and height of tallest stem (distance from mean ground line to base of bud) were recorded at the end of each growing season. The phenology of each species (leaf development, onset and duration of flowering, seed production and dissemination, leaf fall) was checked weekly from mid-April through November 1 for the first two growing seasons and every second week during the third and fourth seasons.

The timing of stem elongation on deerbrush and greenleaf manzanita plants was determined by inserting a small pin at the base of the terminal bud on 15 randomly selected plants in each plot and monitoring growth. Additional pinning of new terminal buds was done as the stems elongated.

A two-way analysis of variance of stem height and crown width (mixed model, no interaction[18]) was applied to test for significant differences between the two species.[19] Statistical significance in all tests was at $\mu = 0.05$. Data were gathered from selected plants measured each year, and where analyses of means from repeated measurements are concerned, the data are not truly independent. The μ levels or type I errors given for various tests apply to each measurement and year separately.

Results

Survival of deerbrush after four growing seasons was 83 percent; that of greenleaf manzanita, 89 percent. Almost all mortality occurred during late summer and fall after fertilization and irrigation had ended. Low soil moisture in summer months, probably exacerbated by damage to roots during outplanting, appeared to be the chief cause of mortality. No seedlings of either species died after the first year.

Deerbrush plants, which had been outplanted as single stems, began to develop multiple stems from the root crown within a few weeks, usually without death of the original stem. More than 89 percent of plants had multiple stems after one season—a proportion that held throughout the study. Greenleaf manzanita seedlings, also outplanted as single stems, remained as single stems during the first growing season. During the second season, new sprouts from the root crown appeared—sometimes after dieback of the original stem, sometimes without dieback. By the end of the second season, 76 percent of plants had multiple stems. This proportion remained constant throughout the study.

By fall 1995, deerbrush averaged 5.6 stems per plant with a range of 1 to 18, and greenleaf manzanita averaged 3.6 stems per plant with a range of 1 to 10. For both species, stem mortality was almost nil during the study. Three deerbrush stems and two manzanita stems died of unknown causes. Statistical analysis indicated that deerbrush had significantly more stems per plant than greenleaf manzanita (root mean square error = 2.86, $F = 17.54$, $P = 0.0001$).

After one growing season, deerbrush plants averaged almost 14 cm tall and after four seasons were more than 102 cm tall (*table 1*). The tallest plants would have been even taller except that they tended to droop a little. Greenleaf manzanita stem height averaged more than 12 cm after one season and more than 63 cm after four seasons (*table 1*). Mean stem height did not differ statistically between the two species after one growing season but did so after two seasons, and continued thereafter. Deerbrush was consistently taller than greenleaf manzanita.

Average crown width of deerbrush was 14 cm after one growing season and more than 130 cm after four seasons (*table 1*). Manzanita crown width averaged almost 11 cm after the first growing season and more than 68 cm after four seasons. Deerbrush crowns were significantly wider than greenleaf manzanita crowns during the entire study (*table 1*).

The height/crown width relationship differed initially between the two species, but then became similar. Deerbrush plants were wider than they were tall throughout the study. Greenleaf manzanita plants were taller than they were wide the first two growing seasons and then became wider than they were tall during the third and fourth seasons.

The phenology of deerbrush and greenleaf manzanita differed in some respects and was similar in others. Flowering was a large difference. Flowers first appeared on deerbrush plants during the third growing season with 42 percent producing a few flowers. By the end of the fourth season, 77 percent had produced flowers. Greenleaf manzanita did not flower during the 4-year study.

Diary entries for spring, summer, and fall 1995 portray the phenologies of deerbrush and greenleaf manzanita. Because we wished to compare the two species, results are presented for each in each season. Deerbrush first began to produce leaves about mid-April in spite of freezing temperatures and skiffs of snow. By April 30, leaves were about 1 cm long and racemes were forming. By May 15 the leaves were about 75 percent developed and shoots on the largest plants were just beginning to elongate. By June 8, leaves were full sized, racemes were fully developed (3 to 24 cm long), and flower buds were opening. Shoots were elongating on about 50 percent of plants

***Table 1**—Mean height and crown width of 62 deerbrush and 67 greenleaf manzanita plants, Mount Shasta Ranger District, 1992-1995*

Item	Year	Species	Mean	Root mean square error	F	P
			cm			
Height	1992	Deerbrush	13.9	10.12	0.81	0.3700
		Manzanita	12.4			
	1993	Deerbrush	47.7	24.16	15.73	0.0001
		Manzanita	31.1			
	1994	Deerbrush	81.4	31.11	39.97	0.0001
		Manzanita	47.1			
	1995	Deerbrush	102.6	35.24	41.21	0.0001
		Manzanita	63.2			
Crown Width	1992	Deerbrush	14.1	8.23	4.29	0.0403
		Manzanita	10.9			
	1993	Deerbrush	74.7	30.07	80.20	0.0001
		Manzanita	27.8			
	1994	Deerbrush	108.9	31.40	125.70	0.0001
		Manzanita	47.7			
	1995	Deerbrush	130.7	32.47	120.45	0.0001
		Manzanita	68.6			

at this time. By June 22 all plants that were going to blossom were blooming. Stem elongation ranged from 5 to 35 cm per plant and averaged about 17 cm from June 9 through June 22.

Buds of greenleaf manzanita began to swell about mid-May and, by June 8, had burst on about 90 percent of plants. Stem elongation on the largest plants was about 5 cm. By June 22 new leaves were fully developed, and stems had elongated about 15 cm (range from 3 to 17 cm) from June 9 to June 22.

The timing of stem elongation was similar for both species during the typically hot, dry summer. Deerbrush finished blooming about mid-July and at least a few seed capsules developed on most racemes. These were promptly stripped from many stems by birds and rodents. By mid-August an estimated 80 percent of capsules had disappeared. All had disappeared or were empty by August 30. Stem elongation decreased rapidly after June 22 but continued until mid-July. Mid-July was the time that some tips of stems appeared dry and began to die, damage to stems from sawflies (Hymenoptera: Tenthredinidae)[20] was noticed, and clipping of lower stem tips began to increase. A few leaves were beginning to dry and shrivel.

Greenleaf manzanita grew well until June 22, but growth then decreased rapidly. No stem elongation was recorded after mid-July. Mid-July also was the time that many small bright red galls became visible on the edges of manzanita leaves. These galls were caused by the manzanita leafgall aphid (*Tamalia coweni* [Cockerell]) (Homoptera: Aphididae).[21] They increased in size and visibility through August 4, but, by September 5, were dry and dull-colored. A few lower leaves began to turn yellow on August 17.

During late summer and fall, clipping of deerbrush stem tips accelerated. A survey on October 26 indicated that 63 percent of plants had one or more clipped stems. However, none was clipped above 90 cm. Rodents were the likely culprits. This same survey noted that 72 percent of plants had lost 10 to 90 percent of leaves. The average leaf loss on these plants was 49 percent. By December 1, 99 percent of leaves had fallen on all deerbrush plants. Every plant, however, retained a few greenish-purplish leaves on stem tips.

In contrast to deerbrush, leaves and stems of greenleaf manzanita remained robust and upright with no observed damage. Only a few lower leaves dropped off in the fall.

Discussion

The pressing need for obtaining developmental data on currently uneconomic plant species and for assessing the competitive potential of fast-growing shrubs suggested that results be reported for both species in this study and that similarities and differences be documented. Both deerbrush and greenleaf manzanita are early successional species that arise from established root crowns and from dormant seeds in the soil. Both species are intolerant of shade and adapted to disturbed areas having at least temporarily high levels of soil water and nutrients.

As to similarities, plants of both species in this study sustained moderate early mortality and almost no subsequent mortality, developed multiple stems on most plants, maintained the initial proportion of plants with multiple stems, and grew rapidly. For differences between species, deerbrush showed the most dynamic development. Its strategy was to develop a clump of stems on most plants during the first growing season; manzanita had a similar strategy, but it did not become manifest until the second season. By the end of the second growing season, deerbrush produced significantly more stems per plant, was taller, and had wider crowns than greenleaf manzanita. Deerbrush also began producing flowers and setting seed during the third growing season, while greenleaf manzanita did not produce flowers or seed during the 4-year study. These differences suggest that deerbrush is the more competitive species. More stems per clump mean a wider clump, and this, plus being taller, allows occupation of a larger area sooner than rival greenleaf manzanita. And being able to produce seed soon after disturbance enables at least some new plants to occupy favorable microsites that quickly become unavailable on good sites.

How did development of the artificially propagated plants in this study compare to that of naturally developed plants (from seed) in young conifer plantations? On a site of similar quality in the northern Sierra Nevada, 4-year-old deerbrush plants averaged 64.1 cm tall at age 4 or were 38 percent shorter than plants in this study. Similarly, naturally regenerated manzanita plants were 28 percent shorter. The comparison, however, is not exact because the naturally seeded plants were growing with extensive competition that, on one hand, denied them site resources, but, on the other, forced them to grow taller to avoid being overtopped.

That deerbrush seedlings were wider than they were tall during the study and that greenleaf manzanita seedlings became wider than they were tall during the last 2 years of the study probably are a function of the near free-to-grow environment of the study area. Had there been more competition, the height/width ratio likely would have changed. Botanists should be particularly interested in knowing that plants of both species develop in this manner in more open environments.

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